SHORTER ARTICLES AND DISCUSSION

DISTRIBUTION OF THE CACTI WITH ESPECIAL REFERENCE TO THE RÔLE PLAYED BY THE ROOT RESPONSE TO SOIL TEMPERATURE AND SOIL MOISTURE

As is very well known, it is the common habit, when referring to the relation of a "plant" to its environment, to mean the subaerial portion only, leaving quite to one side the subterranean parts. That there is little logic in this will be readily acknowledged, although the possible causes are not far to seek. In the first place, for patent reasons, roots do not greatly excite our admiration or curiosity, and thus have received little attention in the field. Further, relatively little experimental work has been done on the roots of plants other than on seedlings and growing in solutions. And besides these conditions which refer immediately to the plant, there is a nearly related one which has to do with its environment, especially with the root environment. The soils and the soil condition of whatever sort are probably more difficult to study, and the results more difficult to express in a manner capable of ready application than the subaerial environment of the plant. However, it has not been its difficulty alone that has been the deterrent in the study of the environment of roots since certain features, for instance the soil temperature, can be easily learned by appropriate apparatus. Could we have a comprehensive series of data touching this feature alone, to mention no other, we should be in possession of a very useful engine for use in comparative studies on causes underlying the distribution of plants, and, further, through it the study of the root-systems of plants, and of their biological value, would be greatly stimulated.

While it is here recognized that the presence of a plant in its environment is an expression of the response of the whole plant to the entire environment, it is necessary, for the purpose in hand, to ignore the responses of the shoots, and to focus our attention for the time on the root relation alone. It can be noted, however, as is very well known, that the activities of the latter may be reflected in those of the former. Such a condition, having inter-

esting possibilities, was observed at the Coastal Laboratory, at Carmel, California, and may be briefly referred to in this place. Among the species growing in the experimental plots at the laboratory are *Opuntia versicolor* and *Fouquieria splendens* from the vicinity of the Desert Laboratory, Tucson, Arizona. Owing to the usual low temperature of the air, and soil, these species generally make little or no shoot growth at Carmel. When, however, the roots of the plants are kept in soil whose temperature is 25–30° C., the shoots remaining in the cool air, not only do the roots grow rapidly, but new shoots and fresh leaves are promptly formed. Without pursuing this phase of the matter further it can be seen that analogous results might occur in nature should the soil conditions, for instance its color or the relation of the soil surface to the incident heat rays,[1] be such as to bring about a relatively warm soil environment. Under such conditions it is clear that only a study of the soil temperatures, and the responses of the roots to soil temperatures, would provide the key to the solution of the shoot behavior and to all of its accompanying results.

It is generally recognized that the soil acts as a reservoir for heat, and that the daily course of soil temperature is unlike that of the air immediately above it. Thus, the roots are subjected to temperature conditions which are quite different from those affecting the shoot of the same organisms. The shoot is warmer by day and colder by night than the root and it is improbable whether the roots of most woody plants are often subject to "optimum" temperature conditions, as must frequently be the case of the shoots. An exception to this statement, however, is to be found in the cacti where the most favorable soil temperatures are of great importance among those environmental features that may be called definitive. The roots of most cacti of the Tucson region, and possibly elsewhere, lie near the surface of the ground. For the most part they are less than 30 cm. deep. Inasmuch as the rate of root growth of the cacti, as will be shown below, is relatively slow at temperatures much under the "optimum," the importance to these plants of a shallow position of the roots will be apparent. It is only in the upper soil horizon that such favoring temperatures are to be found. It is of inter-

[1] Cannon, W. A., "On the Relation of Root Growth and Development to the Temperature and Aeration of the Soil," *American Journal of Botany*, Vol. 2, p. 211, 1915.

est to note, on the other hand, that deeply placed root-systems, such as of *Prosopis velutina,* may have a relatively rapid growth rate at relatively low temperatures.[2] In such a case it is quite possible that the rôle played by root response to temperature in species distribution may be less important, or, at any rate, different from that played by the roots of the cacti, for example, to the distribution of members of that family.

We will now glance at the most striking conditions of soil temperature as they obtain at the Desert Laboratory, where much of the work here referred to has been carried on, before taking up a résumé of the response of the roots of the cacti to the temperature of the soil and the relation this suggests to the general distribution of the family.

Three series of soil thermographic records, which are now being supplemented by others, have been kept at the Desert Laboratory. These relate to three depths, namely, 15 cm., 30 cm., and about 2.6 m. Although the records cover a series of years, it will serve the purpose in hand if we refer to those for the year 1910 only.

The mean maxima and the mean minima temperatures for the three depths will provide sufficient data for interesting comparisons.

At the shallowest depth, 15 cm., the mean maxima temperatures for midwinter and midsummer were 8.1° and 34° C., respectively. The mean minima, for the same seasons, were 3.9° and 30.8° C. At a depth of 30 cm. the maximal range was from 12.2° C., in January, to 33° C., in July, and the minima temperatures, for the same months, 10° and 32.2° C., respectively. It was observed that from June to September, inclusive, the curve of the mean maxima for this depth did not fall below 32.2° C.

At a depth of 2.6 m., the mean maxima temperatures ranged from 18.6° C., in January, to 27° C., in July.

Upon comparing, in a general way, the mean maxima for the different soil depths we see that the shallowest soil is the warmest from April to August, inclusive; that in September and October only the highest temperatures are found at a depth of 30 cm.; and that in late winter-early spring the lowest level is also the warmest.

The relation of the rate of root growth in *Opuntia versicolor,* as representative of the cacti, to different soil temperatures indicates interesting conditions and possibilities, and will be given in the following paragraph:

[2] Cannon, W. A., *l. c.*

Very many experimental cultures, of various kinds, made both at the Desert Laboratory and the Coastal Laboratory, have shown that the growth rate of the roots of *Opuntia*, within limits, varies directly with the temperature. It is relatively slow at 20° C., and most rapid at 34° C. The hourly increase in length of the roots at 20° C. is about 0.3 mm., and at 30° C. it is approximately twice this. Above 34° C., the rate falls off rapidly and ceases at about 42.5° C. Below 20° C., the growth rate is very slow, as, for example, at a temperature of about 16° C. an increase in length of a perfectly normal root was found to be only 1 mm. in 14 hours. The maximum rate, taking place at about 34° C., is about 1 mm. an hour.

Referring back now to the soil temperatures, it will be seen that the roots of this species are exposed to optimum conditions in July and August only, although the soil temperatures for one month before and one month following this period, at a depth of 30 cm., or less, is also high enough for an effective growth rate. The soil temperatures, at this depth, in the other months, and at the lowest level throughout the year, are not sufficiently high for the best root activity. However this may be, we find, in short, that suitable soil temperatures obtain at the depths occupied by the roots of the cacti during four months of the year. But it does not follow that root growth goes on throughout this period for the reason that the foresummer is arid and the shallow soils are impossibly dry, having less than 10 per cent. of moisture. Active root growth of the cacti, in fact, commences with the coming of the summer rainy season, about the middle of July. It is ended by the cooling of the soil in early autumn. The length of the active growing season of the roots of the cacti, therefore, does not usually exceed six or eight weeks.

It is in the response of the roots to the temperature and moisture conditions, as just sketched, that lies the crux of the suggestion offered in this paper, namely, that conditions being otherwise favorable, the cacti, which are shallowly rooted, occur in such regions as have the superficial soils moist at the same time they are suitably warm, and they are wanting where such soil conditions fail.

With the reaction of the roots of the cacti to temperature in mind, it will be instructive to examine briefly the leading climatic features, so far as they affect the case in point, of the regions in which the cacti form a conspicuous portion of the vegetation.

According to Engler and Prantl, the cacti occur mainly in the

dry parts of Mexico, in the portions of the United States which border on Mexico, in eastern and central Brazil, and in portions of the Andes countries. Taking two or three genera as examples, we learn, for instance, that *Cereus* occurs in Mexico, and in the Andes of Argentina and Brazil. *Echinocactus* extends from the southwestern part of our country to Brazil and Chili *Opuntia* is found in Mexico, Peru, Chili, in Central America and in the southwestern portions, especially, of the United States. Although certain species are outside of this range, as especially certain opuntias, where the winters are exceedingly cold, all are subject in summer, when active growth takes place, to conditions which are in rather close accord. A glance at the summer climates of these regions will, I think, establish this point.

In the central part of Mexico, at Tehuacan, the annual rainfall is about 15 inches, most of which occurs in summer, and at Pueblo, 70 miles distant, and at a higher altitude, where the annual precipitation is more than twice that at Tehuacan, 72 per cent. of the rain comes in the warm season. The Tehuacan region has been characterized as being the richest of any known in cacti.[3] At Chihuahua, where the rainfall is 10.86 inches, the amount falling in the summer season is also over 70 per cent.

In the southwestern part of the United States, where the cacti constitute a conspicuous portion of the flora, a relatively large summer rainfall is also reported. At Tucson, for example, the precipitation amounts to 11.74 inches annually, of which 54.7 per cent. is received in July, August, and the first part of September.

Turning now to South America, and without especial regard as to the presence of cacti at the particular stations quoted, we find that over a relatively large area, a large percentage of rainfall is in the warm part of the year. For example, at Matto Grosso, Brazil, the greatest rainfall is in December. From June to August and generally for a month before and after this period, the climate is usually dry.[4]

Along the east coast rain occurs from February to April, June to September being dry. In the Cordilleras of Bolivia and Peru, the rainy period is in December–March, and the climate is dry from April to October. At La Paz, although rain may fall any month of the year, December to February is regarded as being the season of rain.

[3] MacDougal, D. T., "Botanical Features of the North American Deserts," Carnegie Inst. Wash. Pub. 99, 1908.

[4] Hann, "Handbuch der Klimatologie," Bd. II, 1910.

We have supplemental evidence that the cacti grow most successfully in such warm temperate moderately arid regions as have precipitation in the warm season from the work of the Australian commission for the study of certain species which have escaped from cultivation in several countries, especially Australia, and have become a pest.[5] In Queensland and New South Wales species of *Opuntia* constitute a serious weed. At Westward and Rockhampton, Queensland, where the cacti are particularly a nuisance, over 50 per cent. of the annual rainfall occurs in December–March, inclusive. Soil temperature data from Brisbane, depth one foot, show that the mean temperature from October to April is between 22.7° and 27.9° C., and that during the colder portion of the year the mean temperature at that depth is below 20° C.[6]

The commission studied the cactus problem in several different portions of the world, among which were Cape Colony, central and southern India, southeastern and southern South America and the Mediterranean region. It will be instructive to sketch the leading climatic features of definite localities where cacti were found to have escaped cultivation.

In southern Africa, species of *Opuntia* occur in a naturalized condition in the Great Karoo and in the Transvaal. In parts of the former region, as at Graaf Reinet, the species are abundant. At Graaf Reinet, according to Knox,[7] where the total precipitation is 15.29 inches, 63 per cent. occurs in November–March. In the Transvaal, where the escaped cacti are less numerous, the rainfall is 26.94 inches, of which 81 per cent. occurs in November–March.

In northern Africa the cacti escape from the oases very little, and the same is to a degree true of other portions of the Mediterranean region. In Algeria and Tunis, according to Knox, the rains are almost exclusively restricted to the winter season.

In India species are naturalized over a large territory, as, for example, in the Madras Province and in the Panjab. In Madras the prickly-pear has become a formidable evil throughout several districts. At Madras[8] 79 per cent. of the total precipitation takes place in August–September. In the state of Mysore, also, the

[5] Report of the Prickly-pear Traveling Commission, Brisbane, 1914.

[6] "Results of Rainfall Observations made in Queensland," H. A. Hand, 1914.

[7] "The Climate of the Continent of Africa," 1911.

[8] Hann, "Handbuch der Klimatologie," *l. c.*

opuntia is commoon. At Mysore, according to Hann, 81 per cent. of the rainfall is from May to October. At Lahore the prickly-pear is not so abundant as further south, but it occurs escaped, nevertheless. Here the July–August rains comprise 55 per cent. of the total annual precipitation.

In South America the Commission examined naturalized opuntias in portions of Brazil and Argentina chiefly. An important prickly-pear region is northwestern Argentina, where native as well as introduced species of cacti occur in abundance. At Salta there is as good as no rain in the cold season, between May and September. At Tucuman, 69 per cent. of the rainfall takes place between December and March, inclusive (Hann), and at Catamarca, between November and March, inclusive, 81 per cent. of the total annual precipitation occurs.

Without pursuing this phase of the matter further, it would appear, in short, that in regions where cacti are abundant, either native or introduced, rains occur during the warm season. It is not intended to discuss in this place the actual amount of rainfall which falling in the warm season makes the presence of a cactus flora possible. It is well known, however, that the amount of precipitation in regions where cacti occur is extremely unlike, and that it may vary from season to season in any one region. This last, in fact, is one of the leading characteristics of an arid, or semi-arid region. So far as regards the precipitation differences in separate regions frequented by cacti, it is interesting to note that at Rockhampton, Queensland, it is 40.09 inches,[9] while at Phoenix, Arizona, it is 7.06 inches,[10] and that in the former region 20 inches occurs in the warm season, while the amount of summer precipitation at Phoenix is between 0.9 and 2.1 inches, as means of the extremes.[11]

In the Mohave the annual rainfall is 4.97 inches,[12] about two inches less than the mean precipitation for Phoenix. In the Mohave, however, 86 per cent. of the rainfall is in winter, which greatly emphasizes the differences in summer aridity of these regions, and points to a probable reason why cacti are almost

9 "Results of Rainfall Observations made in Queensland," H. A. Hunt, *l. c.*

10 "Botanical Features of North American Deserts," D. T. MacDougal, p. 95, 1908.

11 "Climatology of the United States," A. J. Henry, U. S. Dep. Ag. Bull. Q., 1906.

12 MacDougal, *l. c.*

wholly wanting in the flora of the latter region. From these climatic facts it appears that while soil moisture is a condition *sine qua non* of the presence of the cacti, the range of the actual amount of soil moisture must be very great indeed, so, in short, it results that the temperature is the factor in direct control, thus a very important limiting factor.

Should we sum up, therefore, the factors thus far mentioned as being important among those which determine the distribution of the cacti, we find, in the first place, that the shallowly placed root-system subjects the roots to the greatest possible extremes in soil temperatures, including those that are high, and, at the same time, makes it possible for the plants to advantage from the minimum effective rainfall. Further, an effective growth rate of the roots takes place only at relatively high soil temperatures. And, finally, a certain but highly variable amount of moisture must be present in the soil. Since the *crux* of the matter, however, appears to be the fact that the root-system of the cacti are essentially superficial, there is the additional factor, or factors, which bring about this circumstance. These are at present unproved, but the results of experimental studies, not published, indicate that among them must be included the response to the oxygen supply of the soil.

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THE INHERITANCE OF CONGENITAL CATARACT

In the February number of the American Naturalist there is an article from the Bussey Institution by Jones and Mason[1] in which an attempt is made to show that congenital cataract behaves in heredity as a simple Mendelian recessive. The authors from a study of family histories published by Harman in the "Treasury of Human Inheritance" come to conclusions at variance with those of Bateson and Davenport, which authors they are perhaps unjustly disposed to criticize. The paper is well written and embodies a considerable mass of data, so that the reader not familiar with this particular problem might easily be led to think that the older investigators had really made a mistake in interpretation. The evidence, however, does not seem to

[1] Jones, D. F., and Mason, S. L., "Inheritance of Congenital Cataract," The American Naturalist, Vol. L, No. 590, pp. 119–126, February, 1916.